LIFE HISTORIES, POPULATIONS, AND DISTRIBUTION OF MILLIPEDS

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Millipeds are one of the more abundant and conspicuous groups of invertebrates found in forested regions. Relatively few studies of the biology and ecology of American species have been made. During recent years interest in the group has grown, particularly among foresters and ecologists, with the realization that the soil and humus fauna may play an important role in the dynamics of soil biology and forest communities. In the present report the life histories, habits, and populations of millipeds of several plant communities have been studied. Particular attention has been given to the ecological factors of the environment which appear to function in regulation of the size of the population attained and in the distribution of species.

Milliped populations have been sampled using a one-tenth square meter ring and a folding one square meter quadrat. The former was a circular iron ring of heavy sheet steel 7½ centimeters wide and sharpened on one edge so that it could be readily driven into the soil. The contents of the one-tenth meter ring samples were placed in muslin sacks and returned to the laboratory where they were processed by sieving into a white enameled dishpan. The animals were removed from the contents of the sieve and from the finer material passing through the sieve. The one square meter quadrat samples were taken to a depth of 3 to 4 centimeters, and the material was hand sorted in the field.

Population indices expressed as the number per square meter are used in comparing populations of the various communities. These indices include adults and the later instar stages. Early instar stages were omitted as they tend to occur in aggregations and inclusion of one or more of these aggregations in a set of samples would affect the population index in an irregular manner. An attempt has been made to approach actual or real population values in the indices. The life-histories of the various species, when known, have been considered in determining what portion of the later instar stages should be included. The adults and the last two instar stages have been included in the indices for most species completing their life cycles within approximately one year. A greater portion of instar stages are included in the indices of species having a life cycle of two or more years. Figure 1 for *Pseudopolydesmus serratus* illustrates the differences in the population indices obtained when based on adults and sixth and seventh instar stages and when based on all instar stages; the former index is considered as more nearly representing the stabilized population.

The two sampling methods do not give comparable population indices due to differences in: areal coverage; methods of processing; depth of sampling; habits and reactions of the species to factors of humidity, time of day, intensity of light, rate of air movement, nocturnalism (*Arctobolus* sp.), life history patterns, and other factors which may and probably do affect the surface and near surface activity of some forms. Some species which occupy special microhabitats, such as *Polyzonium bivirgatum, Brachycybe lecontei* and *B. petasata,* and *Androgonathus corticarius,* are not adequately sampled by either of the methods used.

Species-area curves drawn for several stations indicate that 8 or 10 one-tenth square meter ring samples and 6 or 8 one square meter quadrat samples approach an adequate sampling of the more abundant species.

The study is treated in two parts. One part deals with the life history and ecology of *Pseudopolydesmus serratus* and *Scytonotus granulatus.* species found in Wm. Trelease and Brownfield Woods near Urbana, Illinois. The second part is concerned with an investigation of the distribution of milliped populations in different types of plant communities in the Great Smoky Mountains.

In the life history studies of *Pseudopolydesmus serratus* (Say) and *Scytonotus granulatus* (Say) data have been derived from three principal sources: field observations; quantitative sampling; and cultures maintained in the laboratory. The quantitative sampling data have been obtained in part from data accumulated in connection with a research project on populations which has been carried on in Wm. Trelease Woods for over 14 years. Data and milliped specimens from this project have been used for the years January, 1944, through June, 1948. The writer's collections were made from March, 1946, through June, 1948.

Accounts of the post-embryonic development of *Pseudopolydesmus serratus* and *Scytonotus granulatus* are given, completing previous partial accounts. The developmental stages of these species were found to be similar in general pattern to other Polydesmoidea. *P. serratus* has seven instar stages and *S. granulatus* has six instar stages. Further notes on the habits and reproductive activity are given. The occurrence of copulating pairs of these species has been found not to be a reliable index to the time of production of eggs. Adults sexually immature have been found to copulate frequently.

Two major breeding periods of *Pseudopolydesmus serratus* have been found to occur in woodlands in the vicinity of Urbana, Illinois. The first period occurs in spring from March to May, with the peak in April. The resulting offspring pass through the developmental stages and become adults by autumn or late autumn of the same year. They pass the winter

in this stage, become sexually mature and breed the following spring. A second breeding period occurs in June and July. The offspring from this brood reach the late immature stages (fifth, sixth, and seventh instars) by late autumn, pass the winter in these stages and complete their development the following spring. They become sexually mature in June and July and form the breeding population at this time. After breeding, the adult *P. serratus* die out of the population. The data do not indicate that these two populations are separated to the extent of being genetically distinct.

A comparison of population indices, from permanently marked 2500 square meter quadrats, with the degree of slope shown on contour maps of Wm. Trelease and Brownfield Woods, indicates that *P. serratus* is considerably more abundant in Wm. Trelease Woods, a level and more poorly drained woodland, than in Brownfield Woods, a better drained woodland. Within Wm. Trelease Woods higher populations occurred in the areas of poor drainage. *P. serratus* was found to be predominantly a surface inhabitant, living under the leaf litter and is rarely found in the soil proper; thus it is dependent on moist surface microhabitats that remain relatively moist during dry periods. Communities which offer surface microhabitats that remain moist may be more favorable for the survival and maintenance of high population levels.

P. serratus has been found to fluctuate in abundance considerably from year to year. An analysis of the population levels and the composition of the population in Wm. Trelease Woods for the years 1944 through June, 1948, has been made with respect to the deviations of rainfall and temperature from the normal. Years with above normal spring and summer rainfall are accompanied by an increase in population from both the spring and summer reproductive periods (1945). Above normal spring rainfall is accompanied by an increase in the population produced from the spring reproductive period (1944, 1947). Rainfall below normal in the summer period is accompanied by reductions of the population produced from the summer reproductive period (1946, 1947). The early developmental stages appear to be most affected by deviations of rainfall from normal.

Populations of *Scytonotus granulatus* have been analyzed in the same manner as given for *P. serratus*. One breeding period has been found. This occurs in March, April, and May. The adult stage is attained by late autumn, and by the following spring they are sexually mature. Following reproduction in the spring the adults gradually die out of the population. Individual females of *Scytonotus granulatus* have been found to deposit eggs in two, and occasionally three, egg-chambers or nests during a single

reproductive period; this behavior is a variation from the usual pattern in most Polydesmoid millipeds which deposit all the eggs in a single nest or egg-chamber.

Fluctuations in the population of *Scytonotus granulatus* also appear to be correlated with deviations of rainfall from normal. Deviations from normal rainfall appear to be most effective in increasing or decreasing the population when they occur in the spring and summer seasons. These are the periods when eggs are deposited and the millipeds pass through the earlier instar stages. Above normal rainfall is accompanied by an increase in the adult population level (1945). Below normal rainfall for any considerable part of the spring or summer periods results in an adult population decrease (1946, 1947). The peak population level of all larval stages of *S. granulatus* occurred in 1946, due to reproduction from the high adult population in 1945. The highest population levels of both the adults and juveniles of *P. serratus* were reached in 1945. Population fluctuations of *S. granulatus* are of less magnitude than is the case for *P. serratus*. This appears to result from differences in the rate of development and the reproductive capacity of the two species.

The species was found to be somewhat more abundant in Trelease Woods than in Brownfield Woods. *S. granulatus* seems to be less restricted in distribution by factors associated with drainage than is the case with *P. serratus*. A comparison of populations from poorly-drained sites with well-drained sites in Wm. Trelease Woods indicated little difference in the distribution of adults. However, the larval stages appeared to be more abundant in poorly-drained sites. A tendency for this milliped to be frequently associated with rotting logs and accumulations of litter and debris has been noted. During dryer periods the millipeds appear to retreat to these niches.

The investigation of the distribution of milliped populations in the Great Smoky Mountains, near Gatlinburg, Tennessee, was conducted during June and July, 1947. Ten major vegetation types were studied: cove hardwood forests, at 1500 feet, 2600 feet, 3000 feet, and 4000 feet elevations; a beech gap forest, at 5500 feet; a red oak-chestnut forest at 3750 feet; a chestnut oak-chestnut forest and heath at 2700 and 3150 feet respectively; a red oak-hickory forest at 1500 feet; a Virginia pine forest at 1500 feet; a pine heath at 3500 feet; a hemlock forest at 4900 feet; a grassy bald at 5600 feet; a spruce-fir forest at 5900 feet and 5600 feet; and a heath bald at 4900 feet. The majority of these forest types are represented by 15 or more one-tenth meter ring samples and a variable number of one square meter quadrat samples. The red oak-chestnut

forest is represented by only 3 one square meter quadrat samples; the red oak-hickory, by 8 one-tenth square meter ring samples and 12 one square meter quadrat samples; the Virginia pine forest, by 9 one-tenth square meter and 12 one square meter samples. The samples for the majority of stations were obtained on three dates during the two month period.

The distribution of the milliped species and populations has been analyzed by the use of altitude-temperature and mesic-xeric gradients. The mesic-xeric gradient has been determined by the plant composition of each station.

The distribution of the individual species with an indication of the population levels attained are shown in Table I. The distribution of populations of the individual species and of total milliped populations along the mesic-xeric gradient indicates the majority are mesics or submesics.

The following species were present at all altitudes: *Cleidogona caesioannulata, Dixidesmus sylvicolens, Lasiolathus virginicus* (at least up to 5600 feet), *Mimuloria ducilla, Spirostrephon* sp. (at least up to 5600 feet), *Saiulus* sp., and *Brachycybe petasata. Trichopetalum* sp. and *Aporiaria deturkiana* were restricted to altitudes above 4000 feet. Those at the mid-altitudes were: *Nannaria scutellaria* (2500-5500 feet), *Delophon* sp. (2500-3500 feet), and *Striaria granulosa* (2700-6000 feet). The species of low altitudes were: *Apheloria bidens, Arctobolus* sp., and *Brachycybe lecontei.* The distribution of milliped species along the altitude-temperature gradient has been found to vary considerably from species to species. The greatest altitudinal break occurs at approximately 4500 feet, coinciding with the change in forest vegetation from the deciduous and pine forest at the lower altitudes to the spruce-fir forests of the higher altitudes. The occurrence of the deciduous beech gap or beech orchard forest above 4500 feet appears to permit several species of the deciduous forests of lower altitudes to maintain significant populations above this 4500 foot line.

The total milliped populations occurred in the following descending order of abundance: the cove hardwoods forest; the grassy bald; the spruce-fir; the beech gap forest; the red oak-chestnut forest; the hemlock forest; the chestnut oak-chestnut forest; the red oak-hickory forest; the pine forest and heath; and the heath bald. Twenty-one species were represented in the cove hardwood forest with a population index of 215 per square meter. The index for the grassy bald was 185 with two species composing 90 per cent of the population, and the spruce-fir forest had a total population index of 90 with 3 species making up 98 per cent of the population. The index for the heath bald was zero.

TABLE I. CORRELATION OF MILLIPED POPULATIONS WITH PLANT COMMUNITIES

EASTERN FOREST SYSTEM

Cove Hardwood Forest	Beech Gap Forest	Hemlock Forest	Red Oak-Chestnut Forest	Chestnut Oak-Chestnut Forest
Species with 25 per square meter				
Nannaria scutellaria.....S Nopoiulus minutus.....H				
Species with 10 to 25 per square meter				
Cleidogona caesioannulata...C Saiulus sp.....S	Cleidogona caesioannulata...C Saiulus sp.....S	Nopoiulus minutus.....H	Cleidogona caesioannulata...C	
Species with 5 to 10 per square meter				
Striaria granulosa.....C Delophon sp.....C Dixidesmus sylvicolens.....C Lasiolathus virginicus.....C Ptyoiulus sp.....S	Ptyoiulus sp.....S	Cleidogona caesioannulata...C	Dixidesmus sylvicolens.....C Cleidogona caesioannulata...C Delophon sp.....C	Cleidogona caesioannulata...C
Species under 5 per square meter				
Spirostrephon sp.....C Polyzonium bivirgatum.....C Trichopetalum sp.....H Conotyla sp.....? Arctobolus sp.....C Brachycybe lecontei.....C Mimuloria ducilla.....S Brachycybe petasata.....C Apheloria bidens.....S Androgнathus corticarius....C Cambala sp.....? Aporiaria carolina.....?	Lasiolathus virginicus.....C Trichopetalum sp.....H Mimuloria ducilla.....S Aporiaria deturkiana.....S Spirostrephon sp.....C Nannaria scutellaria.....S Striaria granulosa.....C Dixidesmus sylvicolens.....C	Saiulus sp.....S Dixidesmus sylvicolens.....C Spirostrephon sp.....C Polyzonium bivirgatum.....C Brachycybe petasata.....C Aporiaria deturkiana.....S Mimuloria ducilla.....S Lasiolathus virginicus.....C	Saiulus sp.....S Ptyoiulus sp.....S	Dixidesmus sylvicolens.....C Lasiolathus virginicus.....C Striaria granulosa.....C Mimuloria ducilla.....S Delophon sp.....C Spirostrephon sp.....C Polyzonium bivirgatum.....C Brachycybe petasata.....C Saiulus sp.....S Arctobolus sp.....C Apheloria bidens.....S

TABLE I — CONTINUED. CORRELATION OF MILLIPED POPULATIONS WITH PLANT COMMUNITIES

EASTERN FOREST SYSTEM			BOREAL FOREST SYSTEM	
Red Oak-Hickory Forest	Virginia Pine Forest and Pine Heath	Grassy Bald	Mesic Spruce-Fir Forest	Heath Bald
Species with 25 per square meter				
		Saiulus sp. . . . . S Ptyoiulus sp. . . . . S	Trichopetalum sp. . . . . H Cleidogona caesioannulata . . . C	
Species with 10 to 25 per square meter				
Species with 5 to 10 per square meter				
Cleidogona caesioannulata . . . C Lasiolathus virginicus C		Cleidogona caesioannulata . . . C	Aporiaria deturkiana . . . . . S	
Species under 5 per square meter				
Dixidesmus sylvicolens . . . . . C Cambala sp. . . . . ? Spirostrephon sp. . . . . C Juloidea, unidentified . . . . . ?	Juloidea, unidentified . . . . . ? Cleidogona caesioannulata . . . C Arctobolus sp. . . . . C Saiulus sp. . . . . S	Trichopetalum sp. . . . . H Spirostrephon sp. . . . . C Aporiaria deturkiana . . . . . S Dixidesmus sylvicolens . . . . . C Lasiolathus virginicus . . . . . C Mimuloria ducilla . . . . . S	Saiulus sp. . . . . S Mimuloria ducilla . . . . . S Striaria granulosa . . . . . C Polyzonium bivirgatum . . . . . C Brachycybe petasata . . . . . C Dixidesmus sylvicolens C	Cleidogona caesioannulata . . . C

Legend for niche or habitat groups: S = soil inhabiting species; H = organic humus inhabiting species; C = leaf litter layer and cryptozoic species.

The millipeds studied have been placed into three principal niche or habitat groups on the basis of habits associated with their life histories, their occurrence in samples, and the pattern of their distributions in the several plant communities. The niche or habitat groups are: soil inhabiting species; organic humus inhabiting species; and cryptozoic species, living under the leaf litter, under and in decaying logs, under stones and rocks, and in similar situations. These habitats have been designated in Table I by letters.

A correlation between the distribution of milliped species with the various strata or layers of the plant communities has been found. The majority of milliped species had their highest populations in the deciduous forests.

The highest populations of the soil inhabiting species were found in the grassy bald, the cove hardwood forest and the beech gap forest. The grassy bald, in the opinion of the writer, represents a special situation as regards the millipeds. For soil inhabiting animals the conditions are mesic or submesic due to the presence of the deep, rich soil. The herbaceous vegetation, indicating the presence of good soils, was better developed in the grassy bald, cove hardwood forest, and the beech gap forest than in the other communities.

The organic humus inhabiting species had the highest populations in the spruce-fir forest, the cove hardwood forest, and the hemlock forest.

The cryptozoic millipeds had their highest populations in the cove hardwood, the red oak-chestnut, the red oak-hickory, and the chestnut oak-chestnut forests. The cryptozoic group as a whole was poorly represented in the spruce-fir forest and hemlock forest. A correlation appears to exist between the deciduous elements in the shrub, understory tree and tree canopy layers and the distribution of populations of a majority of the cryptozoic milliped species.

The three principal microhabitats are present in the several communities in different proportions. Thus the occurrence in a given community of a high population of a particular milliped species depends upon the good development there of the particular microhabitat with which it is associated.

VITA

Hugh Hanson was born at Lewis, Kansas, on December 16, 1915. He attended elementary and secondary schools at Ness City, Kansas, and was graduated from the Ness City High School in 1933. His undergraduate education was obtained at Kansas State Teachers College, Emporia, where he received the Bachelor of Science in Education degree in 1939. In the academic years 1936-1939 he was employed as an undergraduate laboratory assistant in biology at the Kansas State Teachers College, Emporia. The Master of Science degree was received from the University of Illinois, Urbana, in 1941. During the two academic years 1939-1941 he was employed as a teaching assistant in zoology at the University of Illinois. He was employed as a research assistant to Professor V. E. Shelford, Department of Zoology, University of Illinois, from 1941 until November, 1942, at which time he entered the U. S. Navy and became an epidemiology technician.

He returned to the University of Illinois in March, 1946. During the school year 1947-1948 he was a research assistant to Professor S. Charles Kendeigh, Department of Zoology and Physiology, University of Illinois.

He is a member of Phi Sigma and Sigma Xi and the Ecological Society of America.